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AGGRESSION AND MATING SUCCESS IN MALES OF THE FORKED FUNGUS BEETLE, *BOLITOTHERUS CORNUTUS* (PANZER) (COLEOPTERA: TENEBRIONIDAE)

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Abstract.—The forked fungus beetle *Bolitotherus cornutus* (Panzer), inhabits bracket fungi. Males differ greatly in their body size and in the size of their horns. Evidence is presented suggesting that large-horned males have greater access to fungal feeding sites and mate more frequently than smaller-horned males.

The forked fungus beetle *Bolitotherus cornutus* (Panzer), completes its entire life cycle on polyporoid bracket fungi (Liles, 1956; Pace, 1967). Females plaster single eggs to the surface of the brackets with excrementlike material. Upon eclosing, the larvae bore into the fungus where they feed on fungal tissue. Pupation occurs in the bracket, and, after emerging, the adults live and feed exclusively on the fungal shelf. Adults may reproduce in successive seasons, and specimens older than two years have been recorded in the wild (Pace, 1967). Movement patterns suggest that these beetles are highly sedentary, spending most of their lives on a single tree or even a single fungal bracket (Heatwole and Heatwole, 1968; Brown, unpublished data). Bracket fungi thus represent a resource which is critical to the successful growth and reproduction of this beetle; yet trees infected with fungi are widely scattered, and the feeding activities of both larvae and adults ultimately destroy the fungal brackets.

Unlike the female, the male possesses a pair of horns that arise from the pronotum and extend anteriorly well beyond the head. Horn size is highly variable, ranging from 31% to 80% of the total body length of the beetle.

Males use their horns during two types of aggressive encounters (Pace, 1967; this study). When two males meet on a fungal bracket, they may push each other with their horns butted together, an interaction which may end when one male retreats or is dislodged and drops off the fungus. Alternatively, aggression may result from an encounter between a male and a male-

Table 1. Percent occupation of the experimental fungus block by large-horned males (L) and small-horned males (S) when both L and S were present in the experimental arenas. Probability levels (P) refer to the null hypothesis that paired percentages are equivalent (two-tailed test, Sokal and Rohlf, 1969). Sample sizes are in parentheses.

Observation	% occupation	P
A. At least one of the males was occupying the fungus (395),		
when L alone was on fungus,	36	
when S alone was on fungus.	16	<.001
B. A solitary male was occupying the fungus (206),		
when that male was L,	69	
when that male was S.	31	<.001
C. One of the males and the female occupied the fungus simultaneously (95),		
L was with the female,	78	
S was with the female.	22	<.001

female pair. Mating is preceded by as much as 30 minutes of precopulatory activity during which a male remains mounted on a female so that his head is over her posterior and his posterior over her head. The male then protrudes his aedeagus (which projects onto the female's head or prothorax) and rocks violently from left to right. Solitary males encountering such a precopulatory (or copulatory) pair may attempt to dislodge the mating male. In this instance, the aggressor typically approaches the coupled male and grasps his antagonist by using his pronotal horns and head as forceps. The aggressor may thus successfully pry the courting or breeding male off the female.

Although aggression between males has been observed by several workers (Liles, 1956; Pace, 1967) and has led to the postulation of territoriality in this species, aggressive encounters are relatively rare, and two or more males are found on single fungus brackets in the field. The facts that fungal brackets represent defensible resources critical to reproduction and that the males use horns of variable sizes during encounters with other males suggest a series of experiments designed to examine some of the behavioral interactions between males when food and oviposition sites are limited.

Methods

Twenty-one experimental arenas were constructed by inverting transparent plastic drinking cups (8.75 cm diameter, 7 cm height) over petri dishes. The floor of each chamber was covered by forest leaf litter. A cube of fresh

Table 2. Percentages of courtship and breeding activities in the paired males experiment. F = female; other abbreviations as in Table 1.

Observations	% of courtship	*P*
A. All courtship and copulatory activities (58),		
involving L and F,	79	
involving S and F.	21	<.001
B. Courtship and copulatory activities on the fungal block (30),		
involving L and F,	89	
involving S and F.	11	<.001
C. Courtship and copulatory activities on the chamber floor (28),		
involving L and F,	70	
involving S and F.	30	<.001

bracket fungus (*Ganoderma applanatum* (Pers.) Patouillard), 15.6 cm^3 was mounted on a toothpick pedestal in the center of the chamber, approximately 4.5 cm above the floor. Two males, differing in horn size, and a single female were placed in each chamber. Chambers were maintained at room temperature with ambient lighting in the Mountain Lake Biological Station, Pembroke, Virginia. The positions and activities of the beetles in each chamber were determined at irregular intervals of at least 30 minutes for the next five days. Beetles were scored as being either on or off the fungus and reproductive behaviors were noted. All observations were made between 0900 and 0200 hours, night time observations relying on a flashlight for illumination. After five days, the larger-horned male in each chamber was removed in order to determine the viability of the smaller male (i.e., as a control). Observations continued for an additional four days. Each arena was observed a total of 40 times during the course of the experiments.

Results and Discussion

When both males were present in the experimental arenas, larger males were observed on the fungus blocks significantly more often than were smaller males (Table 1). In fact, solitary larger males accounted for 36% of all observations in which one or both of the males were observed on the fungus. Solitary small males accounted for only 16% of these observations, and both males occurred on the fungus 24% of the time. When the analysis is restricted to those observations in which only one male occupied the fungus, that male was the larger male in 69% of the samples. When only

Table 3. Percentage comparisons of the behavior of small-horned males when large-horned males were present in the experimental arena and after the large-horned males had been removed from the arena. Abbreviations as in Tables 1 and 2.

Observation	Two males present	Small male only	P
A. Total,	(608)	(210)	
when S was on the fungus,	45	58	<.001
when S alone was on the fungus,	16	22	.027
when S and F were on the fungus,	18	36	<.001
when S was courting F.	2	3	.078
B. Courtship and copulatory activities,			
involving either male on the fungal block,	52 (58)	50 (6)	>.10
involving S on the fungal block.	25 (12)	50 (6)	>.10

one of the males was observed cohabiting the fungus with a female, that male was the larger male in 78% of the samples. These observations suggest that larger males obtained increased access to feeding and oviposition sites as a result of their size.

Approximately half of all observed breeding behaviors occurred on the fungus, the rest occurring in the leaf litter. Considering both locations, larger males were observed exhibiting breeding behaviors almost four times as often as were smaller males (Table 2). Furthermore, breeding activities on the fungal block involved larger males eight times as often as they involved smaller males. Breeding activities on the ground involved the larger male more than twice as often as they involved the smaller male.

After the large male was removed, the smaller male appeared on the fungus in a significantly greater percent of the observations (Table 3). For example, whereas smaller males were observed on the fungus in 45% of all observations when both males were present in the arena, they were observed on the fungus 58% of the time when they were the only male present in the chamber. Whereas small males cohabited the fungus with the female in only 18% of the observations when both males were present in the arena, they occurred with the female in 36% of the observations made after the larger male was removed. No significant changes were observed in the mating behavior of small males following the removal of the larger males however. Small males exhibited courtship behaviors as frequently and in the same locations when larger males were present in the chambers and after the larger males had been removed (Table 3).

Actual fighting was observed only once during these observations. In this case, both males were on the leaf litter beneath their fungus, and the female was on the fungus. The fight lasted only a few seconds and consisted of several clashes and butts, followed by the mutual retreat of both males to opposite sides of the chamber.

These results suggest that larger males do have greater access to food and oviposition sites than do smaller males, either because of aggressive interactions or avoidance reactions. Larger males also were observed paired with females more often than smaller males, indicating a direct mating advantage. The observation that the mating activities of small males did not increase when larger males were removed from the arenas may suggest either that small males were not as reproductively capable as larger males or that females discriminate against smaller-horned suitors.

While these observations suggest that larger-horned males are favored over smaller-horned individuals, identification of the independent effects of horn and body size is difficult, since horn length was correlated with body total length (correlation coefficient (r) = .74, sample size = 40, probability of a greater r $<$ .01). The critical experimental alteration of horn size has not yet been attempted, but individual males with broken horns have been observed in the wild, suggesting that such manipulations may be feasible.

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